Museum of Comparative Zoology

US ISSN 0006-9698

Cambridge, Mass.

September 20, 1973

NUMBER 408

A TAXONOMIC COMPARISON OF THE AMERICAN UPOGEBIA (DECAPODA, THALASSINIDEA), INCLUDING TWO NEW SPECIES FROM THE CARIBBEAN¹

DAVID THISTLE²

ABSTRACT. This study examines morphological variability as a means of establishing taxonomically useful characters of American Upogebia. The variability of measured characters was analyzed by regression; the variability of meristic characters was considered in a nonstatistical manner for U. affinis and U. omissa. The analyses make it possible to further differentiate these two species. Relatively invariant and therefore useful characters were combined with characters from the literature to delineate the known species. Three Eastern Pacific-Western Atlantic species-pairs are indicated and interpreted as being the result of speciation by geographic isolation caused by the closing of the Central American seaway. Two new species, U. jamaicensis and U. annae, are described. Upogebia rostrospinosa Bott is redescribed and figured.

Introduction

Twelve species of the burrowing mud shrimp genus *Upogebia* are known from North and South America. Two species, *U. operculata* and *U. rugosa*, are morphologically distinct; the remaining ten species are very similar. A study of the variability of characters in two sympatric species, *U. omissa* and *U. affinis*, was made to find characters of low variability which might be suitable for distinguishing among the ten species.

Upogebia have been found from mean low water to 229 m depth. They occur most often in mud flats but are known from

³This study was submitted as a senior thesis at Harvard College. ²Department of Biology, Harvard University, and Scripps Institution of Oceanography, La Jolla, California 92037.

coarser substrates. Their burrow openings are marked by mounds of material removed during excavation. The animal digs by using the third maxillipeds and carries the particles to the burrow opening with percopods 1 and 2 (Stevens, 1928: 346). Burrows are Y-shaped or may be more complex warrens. The animal feeds by creating currents in the burrow by fanning its pleopods. Food particles are removed by a basket of setae on the inner surfaces of the anterior pairs of percopods. Burrows contain several individuals. In North Carolina, Pearse (1945: 305) repeatedly found egg-bearing females and juveniles in the same burrow.

Twelve species of this genus are known from the Americas: Upogebia affinis from Massachusetts to southern Brazil; U. annae n. sp., U. jamaicensis n. sp. and U. operculata from the Caribbean; U. omissa from Panama and Brazil; U. noronhensis and U. brasiliensis from Brazil; U. pugettensis from Alaska to Lower California; U. rugosa, U. rostrospinosa and U. longipollex from the west coast of Central America; and U. spinigera

from the west coast of Nicaragua to Columbia.

To provide a quantitative estimate of the variability expectable in this group of similar species, I examined in detail two species, Upogebia affinis and U. omissa, using characters selected from the literature and from my own preliminary survey. On the basis of this examination, it was possible to clarify the distinctness of these two species, whose morphological similarity could have been a source of confusion. Also, by assuming that characters useful in separating U, affinis and U, omissa were likely to be useful in separating other related species, I constructed a diagnostic matrix comparing the members of the species-group. This matrix of characters made apparent the close morphological similarity of two Pacific-Atlantic speciespairs, U. rostrospinosa and U. omissa, U. spinigera and U. noronhensis. Upogebia rugosa and U. operculata are distinct from the other American species of *Upogebia* and were not analyzed in detail but they apparently form a third species-pair. The occurrence of these pairs of species appears to be the result of the separation of populations by the closing of the Central American seaway and subsequent differentiation of the isolated segments of each original population.

In the course of this study, two new species were recognized ($Upogebia\ annae\ and\ U.\ jamaicensis$) and were analyzed with those previously known. Their descriptions as well as a redescription of $U.\ rostrospinosa$ Bott are given as an appendix

along with a dichotomous key to the American members of the genus. The synonymy of U. sturgisae Boone with U. spinigera and of U. californica (Stimson) with U. pugettensis after Holthuis (1952: 3) and Stevens (1928: 318) respectively is followed.

Materials and Methods

This study is based on alcohol-preserved museum collections of Upogebia affinis (Say, 1818) and U. omissa Correa, 1968 (see Table 1). Material was obtained from the following sources: Dr. H. W. Levi, Museum of Comparative Zoology, Harvard University; Mr. H. B. Roberts, United States National Museum; Dr. L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. Thomas Biffar, Old Dominion University, Norfolk, Virginia; and Dr. A. L. Castro, Museu Nacional, Rio de Janeiro. Dr. Richard Bott, Senckenberg Museum, loaned to me four paratypes of Upogebia rostrospinosa. I would like to express my thanks to these gentlemen for their kind cooperation.

Specimens were examined with the use of a dissecting microscope. Drawings were made with a camera lucida. Overall length was measured from the tip of the rostrum to the posterior edge of the telson by rotation of the specimen in a clear dish along a rule. This method is accurate to ± 2 mm. Other measurements were made with the use of an ocular grid calibrated with a stage micrometer. Table 2 summarizes the characters used and gives the manner in which they will be referred to in the text. Figure 1 shows the meaning of these characters on diagrams of the animal. The abbreviations used in the text and tables, P1, P2, etc., refer to the first pereopod, second pereopod, etc.

The measured characters were analyzed by regression. This procedure eliminated the effect of variability introduced by differences in the sizes of individuals and allowed the setting of confidence limits, which permitted statistical comparisons. The method used was a nonparametric, graphic procedure which is efficient on small, non-normal samples (Tate and Clelland, 1957, 78-82). In all cases the dependent variable was regressed on overall length. Comparisons between species were made by the use of 90 percent confidence limits, but since the procedure decreases in efficiency with distance from the median, all comparisons were made at the point midway between the x-axis medians of the two lines to be compared. In all cases one is

Table 1. Summary of locality, number of individuals in total sample, number of adults of each sex used, and the range in overall length of the subsample. An asterisk after a locality indicates the presence of at least one ovigerous female. Specimens

obtain length of the subsample. An ascense are a rocardy in access on presence of at teast one original elements of U , omissa from Fortaleza-Ceará are paratypes.	aratypes,			
	Upogeb	Upogebia affinis (Say)		
				Range of
	Sample	Subsampled	Subsampled	overall length
	size	males	females	in subsample (mm)
Wellfleet, Massachusetts	29	5	4	34 - 52
Beaufort, North Carolina*	Ξ	೯೧	9	45 - 60
Miami, Florida*	18	65	9	27 - 43
Mississippi Gulf Coast*	23	0	61	32 - 33
Chandeleur Is., Louisiana	c 1	0	C1	32
Rockport, Texas	c 1	1	1	32 - 33
Cumana, Venezuela*	18	9	4	32 - 60
Total	120	18	25	
	Upogebi	Upogebia omissa Correa		
Limon Bay, Canal Zone, Panama*	21	1	_	34 - 44
Fortaleza-Ceará, Brazil	C1	1	-	27 - 32
Mannanguape Stone Reef, Brazil*	9	¢1	4.	25 - 40
Parahyba River, Brazil	61	0	-	53
Rio de Janeiro, Brazil	7	0	0	0
São Paulo, Brazil	7	60	2	26 - 30
Total	26	7	6	

Table 2. Characters used in the analysis of *Upogebia affinis* and *U. omissa*, and indicated by number in Fig. 1. Each character is referred to in the text and tables by the words in italics.

Number	Character
1	Number of ocular spines
2	Rostral ventral spines
3	Number of spines on epistome
4	Number of spines behind the eervical groove
5	Ventral abdominal spines
6	Serration of uropod distal edges
7	Number of uropodal spines
8	Style of dactylar teeth (P1)
9	Style of teeth on fixed finger (P1)
10	Carpal exterior lateral spines (P1)
11	Number of dorsal palm ridges (P1)
12	Proximal meral spine (P2)
13	Width of the rostral base
14	Rostral length
15	Length of eye stalk
16	Length of rostral lateral teeth
17	Length of sixth abdominal segment
18	Length of telson
19	Width of telson distal margin
20	Width of telson proximal margin
21	Length of fixed finger (P1)
22	Length of dactylus (P1)
23	Length of palm (P1)
24	Width of palm (P1)
25	Length of merus (P1)
26	Width of merus (P1)

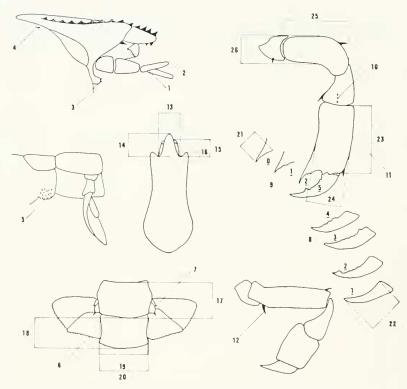


Figure 1. Diagrammatic presentation of characters analyzed, numbered as in Table 2. Underlined numbers are scores for the dentition patterns of fixed finger and dactylus.

testing the position of the lines at this grand median rather than differences in slope (E. W. Fager, personal communication).

When tested for sexual bias in terms of numbers of individuals, none of the collections departed significantly from the null hypothesis of a binomial distribution ($p = q = \frac{1}{2}$) at the 90 percent level. Assuming that the sex ratio is 1:1 in both species, these lots are not significantly biased in terms of sex.

In order to minimize the effect of ontogenetic changes in morphology on interspecific comparisons, this study used the overall length of the smallest ovigerous female in each sample as a criterion for restricting the analysis to adults. This procedure assumed that overall length, age, and maturity were highly correlated so that the probability of females longer than this minimum being adult was large. The overall lengths of males versus females in each sample were such that a Mann-Whitney "U" test (Tate and Clelland, 1957: 89-91) revealed no significant difference at the 90 percent level. Because the samples were not biased in terms of sex (see above) nor were the sexes different in overall size, it seemed reasonable to extend the adult overall length minimum to males. Thus, an adult upogebiid was defined as an individual that was larger, and by inference older, than the smallest sexually mature female present in the sample. In two cases this criterion was set aside for practical reasons. The available specimens of Upogebia omissa contained only two ovigerous females (36, 44 mm), while the lengths of all specimens ranged from 19 to 44 mm (Table 1). Correa (1968) reports adults ranging from 27 to 47 mm. Those individuals smaller than Correa's minimum were considered juveniles, as Correa's range of adult overall lengths was based on 106 ovigerous females. The Wellfleet, Massachusetts, collection contained no ovigerous females. The closest population of U. affinis in overall length is that from Miami and its minimum (28 mm) was used. After the removal of subadults in this manner, subsamples for analysis were taken at random from samples of more than ten individuals.

RESULTS

Measured characters. To provide a quantitative estimate of the variability within a species, Upogebia affinis and U. omissa were analyzed by the regression of 14 measured characters on overall length. Each character was tested for sexual dimorphism by the comparison of 90 percent confidence limits erected about regression lines formed for each sex. For U. omissa none of the 14 characters differed significantly between sexes. In U. affinis fixed finger length (21) and palm width (24) were significantly sexually dimorphic (Figs. 2, 3); the remaining characters were not. Interspecific comparisons using the regression lines for each sex separately revealed no significant difference for either sex on any character. Regression lines formed from both sexes still showed no significant difference between species on any character, excluding characters 21 and 24.

The characters measured contain information about the shape of much of the animal. The results show the two species to be largely indistinguishable in gross morphology, making speculation about the origin and niche separation of these two partially

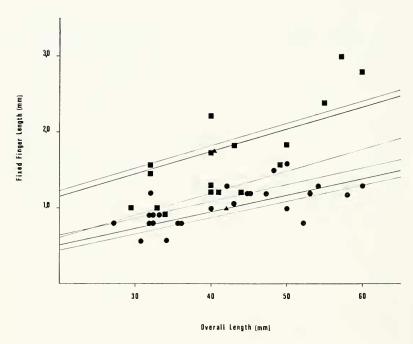


Figure 2. Regression of the fixed finger length onto overall length for males (squares) versus females (circles) of *Upogebia affinis*. The upper triangle is the x-axis median for males; through it passes the best-fit median, regression line. The envelope of lighter lines are 90% confidence limits. The lower triangle marks the female x-axis median point with a similar set of lines.

sympatric species interesting, but to little purpose until their natural history is better known. The analysis does point to problems latent in the use of measured characters in this genus. One must quantify the variability and examine it comparatively before any but the most obvious differences in proportion are given taxonomic weight.

The regression analysis confirmed one feature of taxonomic interest. *Upobegia affinis* has conspicuous sexually dimorphic chelipeds. In the males the cheliped is consistently more robust, larger, and better calcified than in the female. In *U. omissa*, while the males tended to be more variable about the regression line reflecting the occasional dimorphic individual as reported by Correa (1968), there was no significant difference between

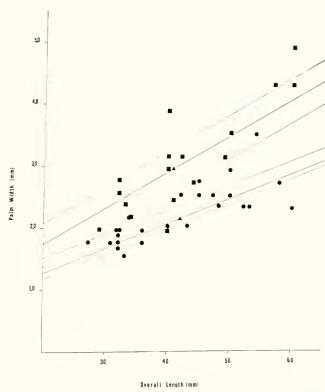


Figure 3. Regression of the width of palm (P1) onto overall length for male (squares) versus female (circles) *Upogebia affinis*. The upper triangle is the x-axis median for males; through it passes the best-fit median, regression line. The envelope of lighter lines are 90% confidence limits. The lower triangle marks the female x-axis median point with a similar set of lines.

sexes. Upogebia affinis is sexually dimorphic in palm width and fixed finger length; U. omissa is not. This dichotomy helps to

distinguish the species.

Meristic characters. Despite this similarity of shape, there are differences between Upogebia affinis and U. omissa. The diagnostic characters of these two species are differences in ornamentation, as are those which distinguish the other species. Table 3 summarizes the results of an examination of 12 of these characters. In it one can see the type of individual and geographic variability present in U. affinis and U. omissa, the features which separate them, and some of those they share.

In delineating *Upogebia affinis* from *U. omissa*, clear disjunctions are most useful. *Upogebia omissa* has ventral abdominal spines and P4 is armed; *U. affinis* does not have these spines. The other characters that show differences between species are less distinct. For a given character, each species has a different dominant state, though some individuals of each species exhibit the character state of the other species. The greater the frequency of the inappropriate character state, the less useful the character, but because of the obvious effect of the interaction between those populations contributing the most specimens to the relative frequency of a character state within a species, these frequencies were not tested statistically.

De Man (1927) redescribed *Upogebia affinis* from a few Carolina specimens. His detailed description agrees with my material. He did not comment on variability beyond two localities. Table 3 can be considered to supplement his description. In addition, the rostrum is not always longer than wide; the telson is rectangular to wider posteriorly; and the upper surface of the telson is not always punctate. De Man refers to reports of *U. affinis* from the "coast of Brazil, Mamanguape stone reef, Parahyba river . . ." On reexamination these specimens were

found to be U. omissa (Table 1).

Correa (1968) described *Upogebia omissa* in detail, including its variability. Beyond those features already discussed, I found the following differences. The eyes are slightly shorter than the rostrum. I have examined a female that is 44 nm long versus a maximum of 35 mm given by Correa. Also, in the table provided by Correa for comparison of *Upogebia affinis* with *U. omissa*, the distinction based on spines on the lower surface of the rostrum is not useful, as *U. affinis* from Venezuela lacks the spines. The protopods of the uropods bear two spines in *U. affinis* from Venezuela rather than one.

tions of characters and scores. A comma separating two character states indicates essentially equal frequency. A character Summary of the results of the meristic characters scored on samples from the following localities: A E) Upogebia Beaufort, North Carolina. C) Miami, Florida. D) Mississippi Gulf Coast; Chande-Forteleza-Ceará, Brazil. H) Mamanguape Stone Reef, Brazil. I) São Paulo, Brazil. Consult Lable 2 and Fig. I for explanastate in parentheses is a low frequency afternate state. A plus sign means the character is present, a minus that it is absent, lem 18., Louisiana; Rockport, Texas. E) Cumana, Veneruela. F-1) U. omissa. F) Limon Bay, Canal Zone, Panama. G) affinis. A) Wellifeet, Massachusetts. B) Fable 3.

Character		U.	U. affinis locality			U.	U. omissa locality	ocality	
	V	23	C	D	ធ	ដ	Ŋ	Н	I
Ocular spines	1 (2)	1 (2)	_	1	I	-	_	I	_
Rostral spines	+	+	+	(-) +	ļ	1	1	1	}
Epistomal spines	1 (0, 2)	П	prod	1 (2)	1, 2	C1	01	2 (1)	01
Cervical spines	1, 2	1, 2	1 (2)	1 (2)	1, 2	i 3	2 (±)	2 (I)	2 (1)
Uropod edge serration	1	+	1	1	+	+	+	+	+
Uropodal spines	I, 2	1, 2	2 (1)	I, 2	01	01	01	61	01
Abdominal spines	panag	I	1	I	1	+	+	+	+
Dactylar teeth	01	10	2 (5)	2 (4)	5	ಸ	ಸ್ತ	5 (2)	5 (2)
Fixed finger teeth	1, 2 (0)	¢1	(0, 3)	0, 2	01	01	++	2 (0)	2 (0)
Palm ridges	01	73	21	73	61	60	90	62)	ഞ
Carpal spincs	oj 60	0.j 60	3, 4 (2, 1)	3 (1, 2)	80, 04	1	П	П	■
Meral spines	+	+	+	+	+	+	+	+	+

The Species of Upogebia

On the basis of the analysis of *Upogebia affinis* and *U. omissa*, I selected characters that had little within-species variability while setting off at least one described species from the others. These characters, coupled with several useful characters from the literature, are presented as a diagnostic matrix showing the interrelationships among the species (Table 4). Characters based on measurements were not included, because the lack of specimens of other American species made it impossible to properly evaluate their variability, except that the ratio of P1 fixed finger length to dactylus length, which is routinely given in the literature, was included.

Table 4 reveals a portion of the interrelationship among the members of the genus in the Americas, and can be used to distinguish among the species. The information presented is from several sources: holotypes of *Upogebia annae* n. sp. and *U. jamaicensis* n. sp., paratypes of *U. omissa* and *U. rostrospinosa*, museum collections of *U. affinis*. The original descriptions of *U. noronhensis* Fausto-Filho 1969 and *U. brasiliensis* Holthuis 1956 were used. For *U. spinigera* (Smith 1871) the original description was supplemented by Holthuis' (1952) redescription. Similarly, for *U. pugettensis* (Dana 1852) de Man (1929) and Stevens (1928) were used.

Upogebia longipollex was described very incompletely and without figures by T. H. Streets (1871) from a Panamanian collection of J. McNeil. Lockington (1878) states that the material ". . . probably came from the Pacific coast of the isthmus." De Man (1928) speculated that U. longipollex might be a junior synonym to U. spinigera (Smith) if differences in spination of the pereopods were the result of differences of the ages of the specimens described. Holthuis (1952) synonymized

 \overline{U} . longipollex with U. spinigera without comment.

The results of this study indicate that leg spination, particularly the P2 meral spine (ventral proximal spine of merus of pereopod 2), is diagnostic at the specific level. Streets, describing spination, states, ". . . third article [carpus] . . . armed with spine above at distal extremity; remaining pairs [of legs] unarmed." *U. spinigera* has a P2 meral spine as well as spines on P3 and P4. It cannot be the same species as *U. longipollex*.

Upobegia longipollex has been included in Table 4 as a good species and adjacent to U, pugettensis to which it seems to be most similar. It appears likely that after an adequate variational

Table 4. Summary of diagnostic differences for A) Upogebia longipollex. B) U. pugettensis. C) U. affinis. D) U. jamaieensis. E) U. rostrospinosa. F) U. omissa. G) U. spinigera. H) U. noromhensis. I) U. brasiliensis. J) U. annae. Consult Table 2 and Fig. 1 for explanations of the characters. A comma separating two character states indicates essentially equal frequency. A character state in parentheses is a low frequency alternative state. "P3 with spines" means that the third percopod bears spines on any segment excluding the dactylus, basis, and coxa.

	•	
	4	
	:	
	٠	
	:	۰
	÷	
	Ľ	
1	_	

	V	æ	C	D	ы	দ	9	Н	I	ī
Ocean	Pacific	Pacific	Atlantic	Atlantic	Pacific	Atlantic	Pacific	Atlantic	Atlantic	Atlantic
Overall length (mm)	21 8	28 38-54 2	27-60	40-50	28	27-60	40	25-30	14-30	32-40
Rostral spines	1	+,+	+	1	ı	1	1	1	J	1
Ocular spines	1 1	(reduced)	1 (2)	4, 5	-	1	-	-	7	1 (2)
Cervical spines	α.	many	1, 2	8-10	2, 3	1, 2	9, 33	1, 2	0	0
Epistomal spines	ſΛ÷	rh.	1, 2	1	3, 3	2	2	<i>(</i>	0	1, 2
Abdominal spines	٨	ļ	1	1	+	+	l	ĭ	I	ı
Ratio: Fixed finger length										
to dactylus length	2.9	Ţ.	∞.	37	7:	rů	7:	6:	6:	6:
Dactylar teeth	5	ນ	2 (5)	C1	5	5 (2)	5	Ç1	rC.	0, 1, 3
Fixed finger teeth	01	_	1, 2	1 (2)	C1	2 (0)	1, 2	7	-	2 (1)
Pl palm cross section	Λ,	squared	squared	squared	ovoid	ovoid	ovoid	ovoid	Λ.	ovoid
Palm ridges	0	2	C1	61	60	ಲ	85	60	01	0
P2 meral spine	[I	+	+	+	+	+-	+	1	1
P3 with spines	I	1	+	+	+	+	+	+	+	+-
P4 with spines	1	l	I	I	1	+	+	1	1	ı
P5 with spines	1	I	ł	I	I	Į	1	+	1	Į
Uropodal spines	۸	-	1, 2	1 (2)	C1	2	23	C1	1	_
Serration of uropod edges	ο.	+	+	+	+	+	+	+	+	+

study of *U. pugettensis* (1852) has been performed, *U. longi-pollex* (1871) will be synonymized under that species, but until the Pacific American upogebiids become better known, *U. longi-pollex* should be maintained.

American upogebiids seem to show examples of speciation by geographic isolation. In Table 4 are two cases where a pair of morphologically very similar species are separated by Central America. Upogebia rostrospinosa from El Salvador is most closely related to U. omissa from Panama and Brazil; U. spinigera from the Gulf of Panama to U. noronhensis from northern Brazil. Upogebia rugosa from the Gulf of California and U. operculata from Barbados are a third example. An interpretation of this evidence is that in each of these cases a single species existed in tropical waters before the close of the Central American seaway. After this event the Atlantic and Pacific populations no longer shared a common gene pool and evolved separately. Under somewhat different selective pressures each population became differentiated while retaining a basically similar morphology within a species-pair. Thus the model of speciation by geographic isolation appears to explain the occurrence of species-pairs in *Upogebia*.

Conclusions

A study of the variability within two species of *Upogebia* has shown measured characters to be of uncertain taxonomic value. Relatively invariant and taxonomically useful characters have been used to help demonstrate the distinctness of ten known species.

It is extremely likely that further collecting will lead to the discovery of additional species. Their description as well as a fuller understanding of the biology and distribution of each species will have to be achieved before one can come to a biologically real understanding of speciation in this group.

ACKNOWLEDGMENTS

I would like to thank Herbert W. Levi, under whose supervision the project was carried out, and all those who aided me in the course of the study. L. B. Holthuis and T. Biffar helped formulate the problem. The following people have read and criticized the manuscript during its several phases: H. W. Levi, T. Biffar, K. Boss, E. E. Williams, S. J. Gould, R. R. Hessler,

W. Newman, J. Sepkoski, P. Jumars, and M. Burkenroad. The Museum of Comparative Zoology provided the facilities for the research.

Portions of this paper were submitted to the Department of Biology, Harvard University, as partial fulfillment of the requirements for the degree of Bachelor of Arts.

References

- Bott, R. 1955. Dekapoden (Crustacea) aus El Salvador. Senckenbergiana Bio., 36: 47-72.
- CORREA, M. M. GOMES. 1968. Sôbre as espécies de "Upogebia" Leach do litoral Brasieiro, com descrição de uma espécie novo (Decapoda, Callianassidae). Revista Brasileira do Biologia, 28: 97-109.
- Dana, J. D. 1852. Conspectus of the Crustacea of the Exploring Expedition under Capt. C. Wilkes, U.S.N. Proc. Acad. Nat. Sci. Philadelphia, 6: 10-28.
- FAUSTO-FILIIO, J. 1969. *Upogebia noronhensis*, nova espécie de Crustáceo do Brasil (Crustacea, Decapoda, Callianassidae). Arq. Ciên. Mar., 9(1): 1-7.
- Haswell, W. A. 1881. Description of some new species of Australian Decapoda. Proc. Linn. Soc. New South Wales, 6: 750-763.
- HESSLER, R. R. 1970. The Desmosomatidae (Isopoda, Asellota) of the Gay Head-Burmuda Transect. Bull. Scripps Inst. Oceanography, 15: 1-185.
- HOLTHUIS, L. B. 1952. Report of the Lund University Chile Expedition 1948-49. On two species of Crustacea Decapoda Macrura from the N.W. coast of South America. Acta Univ. Lund. N.F. Avd. II, 47(9): 1-11.
- LOCKINGTON, N. W. 1878. Remarks upon the Thalassinidea and Astacidea of the Pacific coast of North America. Ann. Mag. Nat. Hist., Ser. 5, 2: 209-304.
- MAN, J. G. DE. 1927. A contribution to the knowledge of twentyone species of the genus Upogebia Leach. Capita Zool., 2(5): 1-58.
- lected by the Siboga Expedition with some remarks on the Laomediidae. Siboga Expedition Reports 39a⁶, part 7: 1-187.
- Expedition L. On a small collection of Decapoda . . . Dansk Naturhistorisk Forening, Copenhagen. Videns. Meddel., 87: 105-134.

Pearse, A. S. 1945. Ecology of *Upogebia affinis* (Say). Ecology, 26(3): 303-305.

SAY, T. 1818. An Account of the Crustacea of the United States. J. Acad. Nat. Sci. Philadelphia, 1(2): 241.

SMITH, S. F. 1871. List of the Crustacea collected by J. A. McNeil in Central America. Rep. Peabody Acad. Sci. for 1869: 87-98.

STEVENS, B. A. 1928. Callianassidae from the west coast of North America. Pub. Puget Sound Biol. Sta., 6: 315-369.

STREETS, T. H. 1871. A catalogue of Crustacea from the Isthmus of Panama. Proc. Acad. Nat. Sci. Philadelphia, 23: 238-243.

TATE, M. W., AND R. C. CLELLAND. 1957. Nonparametric and Short-cut Statistics. Danville, Ilinois: Interstate. 171 pp.

APPENDIX

Upogebia jamaicensis n. sp.

Figure 4

Male holotype from Montego Bay, Jamaica. USNM #41748. The species is named for the type locality. Overall length is 50 mm.

Diagnosis. Upogebia with 4–5 ocular spines; 8–10 spines behind cervical groove laterally; rostral ventral surface unarmed; P2 with strong proximal ventral spine on merus; 1 epistomal spine. For relationships to American species see Table 4.

Upogebia jamaicensis is most closely related morphologically to U. spinifrons (Haswell, 1881) from Australia. Much of the cephalon spination is similar in the two species. Following de Man (1927), U. spinifrons has the rostral ventral surface armed, the dorsolateral extensions of the carapace without tubercles, and with 2 epistomal spines. Upogebia jamaicensis has the rostral ventral surface unarmed, tuberculate dorsolateral extensions, and 1 epistomal spine. There are differences in number of P1 palm ridges and P2 meral spines. No other described species has 4–5 ocular spines.

Description. A slash separating 2 measurements indicates the ratio of the first to the second. For a discussion of the use of ratios in taxonomy, see Hessler (1970: 7). LENGTH: 40–50 mm. CEPHALOTHORAX: Rostral basal width/rostral length is 0.6–0.8. Length rostral lateral teeth/rostral length is 0.3–0.5. Dorsolateral extensions of carapace with 10–12 spines (becoming spinules posteriorly). Eye length/rostral length is 0.5. ABDOMEN: Segmentation typical of genus. Sixth segment width/length is 1.4. Telson width/length is 1.0–1.2. Telson with

proximal transverse carina, median groove, and wrinkled surface. Pereopops: P1: Fixed finger length/dactylus length is 0.3-0.7. Dactylus with large tooth laterally and lesser tubercles distally; large distal tooth on cutting edge with lesser teeth proximally. Fixed finger with 4-6 denticles on cutting edge. Palm width/length is 0.4-0.6. Palm ovoid in cross section. Palm spination: dorsally 2 ridges, outer of spines, inner of spinules. Exteriolateral surface with 6 spines; interiorly 1 distal spine. Carpal spines: 1 large ventrally, 1–2 exteriorly. Dorsally 1 major spine distally with row of 4-6 behind it; 2 exterior, 1-2 interior to it. Meral width/length is 0.3-0.5. Meral spines: 1 distodorsal spine, 6-7 spines on ventral margin. P2: Carpus with distal spine dorsally and ventrally. Merus with distodorsal and proximoventral spines. P3: Merus with 2 distodorsal spines: ventral margin with 4-6 spines, many tubercles. Ischium with 1 spine. P4: Merus of holotype with spine on ventral margin, absent in paratypes. PLEOPODS: Endite of 2-5 enlarged, squarish. UROPODS: 1 spine on interior protopod, tubercle on exterior protopod; distal edges denticulate.

In female, width rostral base/rostral length is greater, P1

dactylus shorter, cheliped less robust.

Range. Jamaica. Four specimens examined. Features of types are: holotype without left P4, right P2, P3. Paratype, female, USNM #138897, same locality, left of carapace damaged. Paratype, female, USNM #138896, same locality, right P1 missing.

Upogebia annae n. sp.

Figure 5

Female holotype: R/V OREGON, sta. 5421, Bahama Isl., lat. 20°54′N, long. 73°36′W, 125 fathoms (229 m). USNM #138892. The species is named for my wife, Anne. Overall length is 25 mm.

Diagnosis. Upogebia with 1, 2 ocular spines, no spines behind cervical groove, P1 fingers of claw equal, P1 with no ridges on dorsal surface of palm. P2, P3, P4 with elongate merus.

Upogebia annae is most closely related to U. brasiliensis. Upogebia annae differs in having no dorsal P1 palmar ridges and no epistomal spines. In U. brasiliensis the merus width/length ratio of P2 is 0.33, of P3 is 0.41, and of P4 is 0.30; in

U. annae that of P2 is 0.20, of P3 is 0.21, and of P4 is 0.22. See Table 4 for comparison to other American species.

Description. A slash separating 2 measurements indicates the ratio of the first to the second. LENGTH: 32-40 mm. CEPHALOTHORAX: Rostral basal width/rostral length is 0.8-0.9. Length rostrolateral teeth/rostral length is 0.2. Dorsolateral extensions of carapace with 10-12 spines (becoming spinules posteriorly). Eye length/rostral length is 0.1-0.3. ABDOMEN: Segmentation typical of genus. Sixth segment width/length is 1.0–1.2. Telson width/length is 0.9–0.10. Telson with proximal transverse carina, median groove, and wrinkled surface. PEREOPODS: P1: Fixed finger length/dactylus length is 1.0. Dactylar row of tubercles variable. Fixed finger with 4-6 denticles on cutting edge. Palm width/length is 0.3-0.5. Palm ovoid in cross section. Carpal spines: distally, one each ventrally, exteriorly, dorsally; dorsal spine with 3-5 above it, 2 interiorly, 2 exteriorly. Meral width/length is 0.3. Merus with distal dorsal spine, 4–6 spines on ventral margin. P2: Carpus with dorsal, ventral distal spines. Merus with distal dorsal variable tubercles on ventral margin. P3: Carpus, ventral distal spine, variable. Meral ventral margin with 2-3 spines, many tubercles. PLEOPODS with oval endite. UROPODS with small spine on protopod.

In female, uropodal exopod extends beyond telson. Males with robust P1, more highly calcified, uropod edges finely denticulate.

Range. Known only from types.

Features of types. Holotype discolored in branchial area. Male paratype, R/V OREGON sta. #5421, USNM #138893, same locality as holotype, left P3, right P5 damaged. Male paratype, R/V SILVER BAY sta. #5158, USNM #138894, Bahama Isl. lat. 19°55.5′N, long. 71°07′W, 100 fathoms (183 m), right P4, P5, left P3, P5 missing.

Upogebia rostrospinosa Bott 1955

Figure 6

Female holotype from Puerto el Triunfo, El Salvador. Senckenburg Museum #2116.

This redescription is based on an examination of one female paratype. Differences from the original description should be noted. No evaluation of variability is possible.

Diagnosis. Upogebia with 1 ocular spine, P2 meral spine, spinules on ventral surface of first abdominal segment, no spines

on P4, spines on telson transverse ridge.

Upogebia rostrospinosa is most closely related to U. omissa on the basis of the ventral abdominal spines. U. rostrospinosa differs in having no spines on P4 while U. omissa lacks the spines on the telson. See Table 4 for comparison to other

American species.

Description. A slash separating 2 measurements indicates the ratio of the first to the second. All measurements refer to the paratype. Length: 28 mm. Cephalothorax: Rostral basal width/rostral length is 0.6. Length rostrolateral teeth/rostral length is 0.3. Dorsolateral extensions of carapace with 9-10 spines (becoming spinules posteriorly). Eve length/rostral length is 0.75. ABDOMEN: Segmentation typical of genus. Sixth segment width/length is 1.3. Telson width/length is 1.2. Telson with proximal, 8-spined transverse ridge. PEREOPODS: P1: Fixed finger length/dactylus length is 0.7. Palm width/length is 0.53. Palm ovoid in cross section, 3 dorsal rows of hairs, 1 external. Carpal spines: 1 ventral distal, 1 exterior distal, 1 dorsal distal with a row of 4 behind it. Meral width/length is 0.5. Merus with 1 distal dorsal spine, 3 on ventral margin. Ischium with 1 spine. P2: Carpus with distal spinule dorsally and ventrally. Merus with distal dorsal spine; proximal ventral spine. P3: Merus with 3 spines on ventral margin, 4 spinules on exterior proximal surface. PLEOPODS with clongate endite.

No males known.

Range. Known only from type locality.

Remarks. Bott (1955) mentions four paratypes (SMF #2117). I have examined these and three do not fit the description of the holotype. The discrepancies are in characters that I have found to be diagnostic, and I believe that these three specimens cannot serve as representatives of Upogebia rostrospinosa.



Figure 4. Upogebia jamaicensis n. sp. male holotype: A) habitus, B) A1, C) pleopod 2, D) sixth abdominal segment and telson, E) percopods 1–5, F) female pleopod 1 (paratype), G) cephalothorax and right cheliped, H) A2. Hairs and setae omitted. Scale lines equal 2 mm.



Figure 5. *Upogebia annae* n. sp. female holotype: A) habitus, B) A2, C) percopods 1–5, D) female pleopod 1, E) A1, F) sixth abdominal segment and telson, G) pleopod 2, H) cephalothorax and right cheliped. Hairs and setae omitted. Scale lines equal 2 mm.

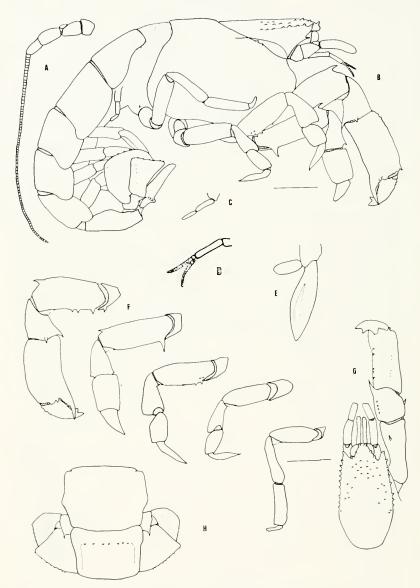


Figure 6. Upogebia rostrospinosa Bott female paratype: A) A2, B) habitus, C) female first pleopod, D) A1, E) pleopod 2, F) pereopods 1–5, G) cephalothorax and right cheliped, H) sixth abdominal segment and telson. Hairs and setae omitted. Scale lines equal 2 mm.

Key to the American Species of Upogebia

1.	а. b.	Telson distal margin conspicuously wider than proximal margin 2 Telson essentially rectangular
2.	∗a.	Rostrum armed dorsally with "two strong spines"; Caribbean U. operculata
	b.	Rostrum "beset with small tubercules and hirsute" dorsally; Pacific, Central America
3.	а. b.	First abdominal segment spined ventrally
4.	a. b.	P4 with spines (see Table 4 caption); Atlantic, Panama to Brazil
5.	а. b.	P2 with proximal meral spine
6.	a. b.	P1 propodus with two ridges dorsally
7.	a. b.	Having one or two ocular spines; Atlantic, widespread $U.$ affinis Having four or five ocular spines; Caribbean $U.$ jamaicensis
8.	а. b.	P4 with spines, P5 unspined; Pacific, Central America to Colombia
9.	а. b.	P3 with spines 10 P3 without spines 11
10.	a.	Epistome spined, P2, P3, P4 with elongate merus; Caribbean
	b.	Epistome unspined; Atlantic, Brazil U. braziliensis
11.	a.	PI propodus with two ridges dorsally; Pacific, Alaska to Lower California
	b.	P1 propodus with no ridges dorsally; Pacific, Central America U. longipollex

^{*}The present distinction between these two species is probably semantic; they are badly in need of redescription.